

PALAEOECOLOGY, TAPHONOMY, AND DATING OF PERMO-TRIASSIC REPTILES FROM ELGIN, NORTH-EAST SCOTLAND

by MICHAEL J. BENTON *and* ALICK D. WALKER

ABSTRACT. Three Permo-Triassic reptile faunas and one footprint fauna are known from the area of Elgin, north-east Scotland. The footprints are probably Permian in age and they indicate an assemblage of mammal-like reptiles. The mammal-like reptiles, pareiasaur and procolophonid from the Cutties Hillock Sandstone Formation (new name) are probably latest Permian in age. They were found at the base of an aeolian unit, just above pebbly sheet-flood deposits. The Lossiemouth Sandstone Formation is dated as Lower Norian on the basis of its varied reptile fauna. This fauna shows affinities with northern and southern hemisphere faunas of its time, and contains Britain's oldest dinosaur, the coelurosaur *Saltopus*. The Lossiemouth reptiles (c. 130 individual animals from four or more localities) were apparently preserved at the bases of barchan dunes and many of them just above flood plain deposits. Most of the skeletons are well preserved in articulation and only a few show disturbance, possibly by scavenging. The fauna consisted of *Hyperodapedon* and *Stagonolepis*, two moderate-sized herbivores (25% each), a selection of small omnivores: *Leptopleuron* (23%), *Brachyrhinodon* (9%), *Scleromochlus* (5%), and *Erpetosuchus* (2%), and a medium-large carnivore, *Ornithosuchus* (10%) and a small carnivore, *Saltopus* (1%). Some of the smaller animals show adaptations to living on sand. The last reptile fauna, from the Rhaetic of Linksfield, consists of odd bones of marine reptiles.

VERTEBRATE palaeontologists who study Mesozoic reptiles often concentrate on individual genera and do not record information on faunas. This paper presents information on the Elgin reptile faunas that we have gathered by personal observation of the specimens and the geology, and by studying unpublished documents and the scattered published literature.

Two main faunas of fossil reptiles are known from the neighbourhood of Elgin, north-east Scotland. The earlier, from the Cutties Hillock Sandstone Formation (defined below; probably latest Permian) consists of two genera of mammal-like reptiles, a pareiasaur and a procolophonid and the later, from the Lossiemouth Sandstone Formation (late Triassic) comprises at least four genera of thecodontians, a rhynchosaur, a sphenodontid, a procolophonid, and a coelurosaur dinosaur. A third fauna from the Rhaetic of Linksfield contains a few marine reptile bones. The Hopeman Sandstone Formation (in the restricted sense proposed in this paper, see below) has also yielded a fauna consisting of two or three kinds of footprints. Both main faunas are unusual in showing close affinities with those of southern continents as well as with those of the rest of western Europe and North America. Both faunas are also unusual in that the remains are preserved in aeolian deposits, clearly not the natural habitat of the majority of the animals.

The aims of this paper are fivefold: to review the composition of the faunas; to consider the sedimentology and environments of the reptile beds; to discuss the taphonomy of the remains; to assess the ecology of the late Triassic reptiles; and to review the relationships and age of the faunas. Most of the data have never been published before, and it is hoped that this paper will provide a useful summary of the Elgin reptiles and their environments. The taphonomic observations are original and should be of value for comparison with other aeolian deposits. Most attention will be devoted to the late Triassic fauna because of the larger number of remains, and its greater importance in Triassic faunal development.

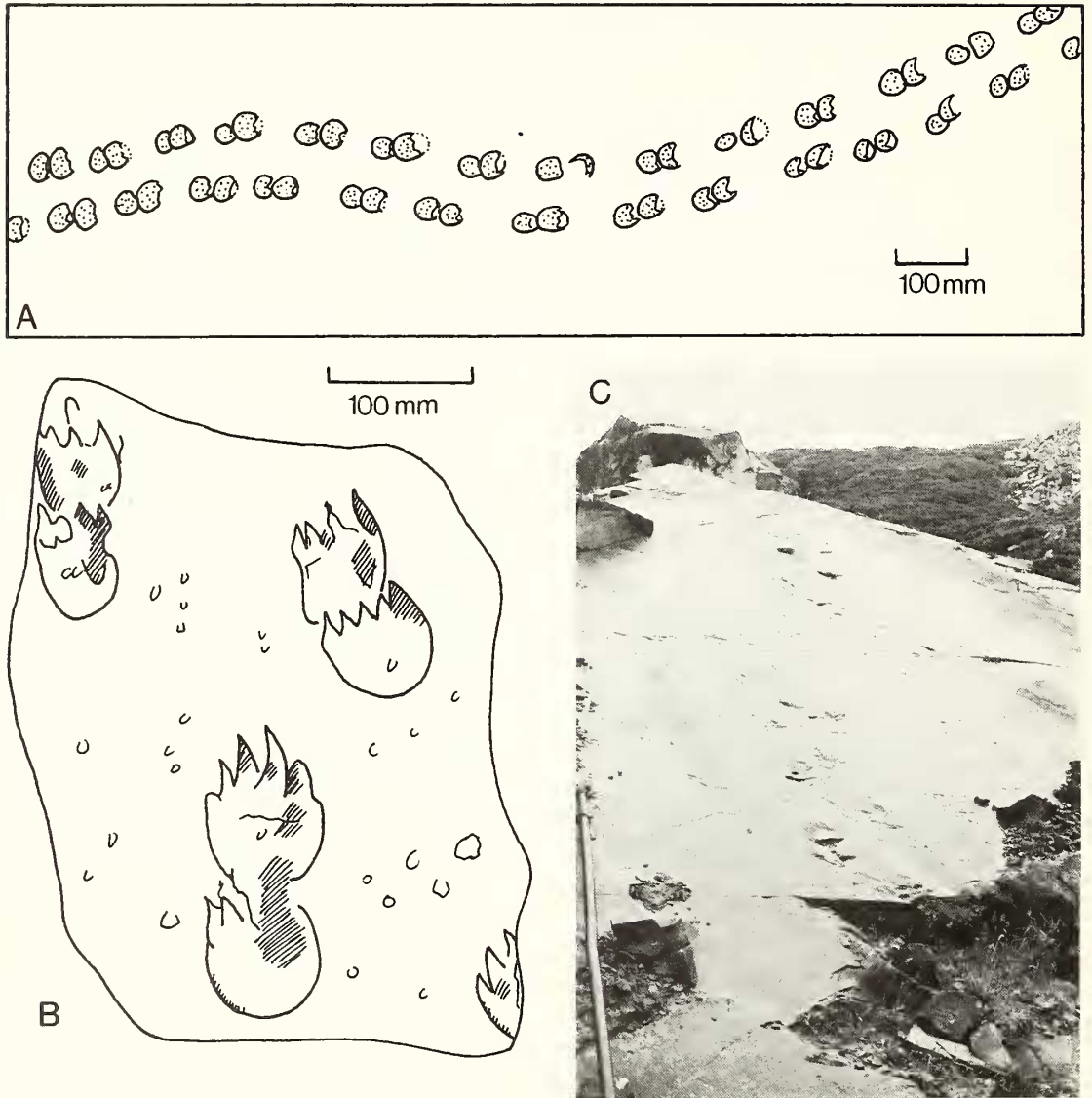
Repository abbreviations used in this work are: BMNH, British Museum (Natural History); EM, Elgin Museum; GSE, Geological Survey Museum (Edinburgh); GSM, Geological Survey Museum (London); MM,

Manchester Museum; NUGD, Newcastle University, Geology Department; RSM, Royal Scottish Museum, Edinburgh.

THE FAUNAS

Footprints from the Hopeman Sandstone Formation

At least two kinds of footprint have been identified from the Hopeman Sandstone Formation. Type A (text-fig. 1A) (roughly circular, impressions 30–40 mm long, stride length 110–120 mm, width



TEXT-FIG. 1. Reptile footprints from the Hopeman Sandstone Formation, near Elgin (?late Permian). A, small prints, after Brickenden (1852); B, medium prints, *Chelichnus megacheirus*, after Huxley (1877, pl. 14); C, large prints, field photograph. A, B from Masonshaugh Quarry; C from Clashach Quarry. Scales are shown for A and B; C shows tracks which are 100–150 mm wide and have a stride length of 700–800 mm.

of trackway 80–90 mm, no sign of toe marks) is represented by a slab collected in 1850. This was the first fossil from Elgin recognized as reptilian, and the trackway was initially interpreted as having been formed by a tortoise (Brickenden 1850, 1852).

Numerous slabs of larger footprints (Type B, text-fig. 1b) were collected after that (Beckles 1859; Huxley 1859b; Hickling 1909). The fore- and hind-foot were clearly different. The print of the fore-foot is semicircular, about 40 mm long and 60 mm wide, with traces of four or five claws at the front. The print of the hind-foot is larger, about 90 mm long and 80 mm wide, with traces of five claws at the front. The prints overlap in pairs, and stride length was 300–400 mm. These were named *Chelichnus megacheirus* Huxley 1877. Larger specimens (print 170 mm long, 140 mm wide) were figured by Huxley (1877, pl. 15, fig. 6) and some similar tracks may still be seen on a large slab at Clashach Quarry (NJ 163702). These large tracks measure 150–250 mm long and 100–150 mm wide, and the stride length is 700–800 mm (text-fig. 1c). A possible third kind of track was described from the coast by Huxley (1877) and Hickling (1909, pl. 2, figs. 7, 8) and from Cutties Hillock (Watson and Hickling 1914). This is supposedly distinguished by having broader toes than Types A or B, but the generally smudged preservation of most specimens makes such a distinction inadvisable. The Hopeman footprints were probably formed by two or more mammal-like reptile genera, possibly dicynodonts (Haubold 1971).

Reptiles from the Cutties Hillock Sandstone Formation

Reptile bones were collected from a quarry on Cutties Hillock in 1884, and some nearly complete skeletons were obtained in 1884 and 1885 (Judd 1885, 1886a, b; Traquair 1886). Three genera were described by E. T. Newton (1893): *Gordonia*, *Geikia*, and *Elginia*.

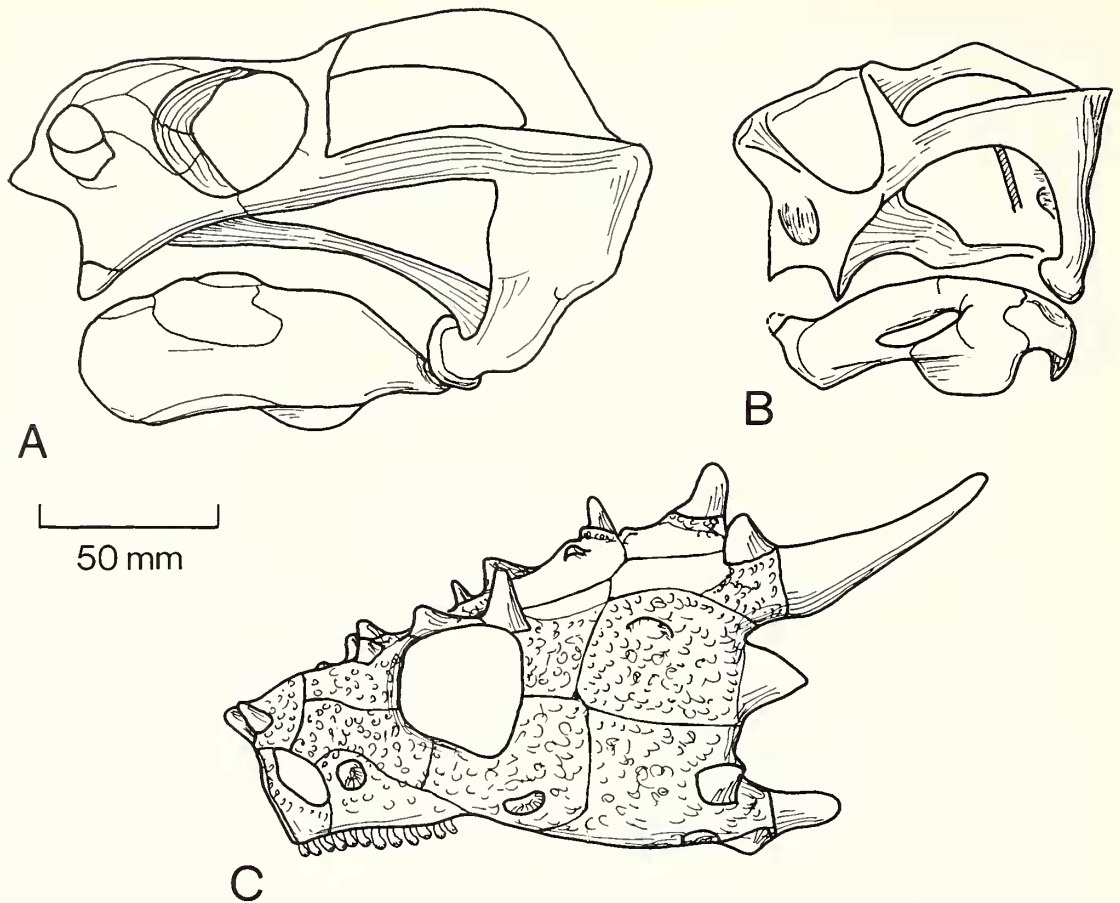
Gordonia and *Geikia* are dicynodonts, a group of herbivorous mammal-like reptiles most of which had no teeth except for a 'tusk'. *Gordonia* (text-fig. 2A) is represented by remains of the skulls and skeletons of eight to thirteen individuals, and four species were originally described, although they are perhaps all synonymous (Walker 1973). *Gordonia* had a heavy broad skull, 100–180 mm long, and it was clearly provided with powerful jaw muscles. The relationships of *Gordonia* are uncertain: Cluver and King (1983, p. 268) state 'possibly related to *Kingoria* or *Dicynodon*'. The single specimen of *Geikia* (text-fig. 2B) is unusual for its short, broad skull which was about 95 mm long (Newton 1893). *Geikia* has no teeth at all and the snout is box-like. Rowe (1980) has redescribed the specimen and assigned it to the family Cryptodontidae with a selection of late Permian dicynodonts from South Africa and Zambia. He also placed '*Dicynodon*' *locusticeps* from Tanzania in the genus *Geikia*, and noted that the closest relative of *Geikia* is *Pelanomodon*. Cluver and King (1983) placed *Pelanomodon* in the new Family Aulacephalodontidae, and Cruickshank and Keyser (1984) have confirmed this assignment of *Geikia*.

Elginia was a pareiasaur with a remarkably spinescent skull (text-fig. 2C). The 210 mm long holotype skull is broad and covered with rough pits and spines of various sizes. The teeth are leaf-like in shape, and *Elginia* was probably a herbivore. Other pareiasaur remains include vertebrae and a sacrum probably belonging to the holotype as well as an undescribed partial skeleton and skull.

A fourth reptile from Cutties Hillock is represented by a specimen that was described by Newton (1893, pp. 461–462, pl. 33, fig. 5) as a tail of ?*Gordonia*. This specimen consists of seven dorsal vertebrae, the blades of two scapulae and the blade of an ilium of a procolophonid (Walker 1973). Finally, remains of an un-named dicynodont were collected from nearby Knock of Alves (or York Tower) Quarry in 1953 by A.D.W.

Reptiles from the Lossiemouth Sandstone Formation (Table 1)

A slab containing scutes of the thecodontian reptile *Stagonolepis* (text-fig. 3A) was the first fossil found in the Elgin Permo-Triassic, but it was initially interpreted as a large ganoid fish (Agassiz 1844). Later finds of limb-bones led to its interpretation as a reptile (Huxley 1859a, b), and in particular as an ancestral crocodile (Huxley 1875, 1877). More recent study (Walker 1961) has shown



TEXT-FIG. 2. The reptiles of the Cutties Hillock Sandstone Formation of Cutties Hillock Quarry, near Elgin (?latest Permian–early Triassic). Skulls of A, *Gordonia*; B, *Geikia*; and C, *Elginia*, all drawn to the same scale. (A, after Newton 1893; B, after Newton 1893 and Rowe 1980; C, after Newton 1893 and original.)

that it was an aetosaur—a probable herbivore. *Stagonolepis* is represented by skull and skeletal remains of thirty or more individuals which were up to 2.7 m long. The snout had a curious blunt end, probably for digging, and the teeth were peg-like. *Stagonolepis* was shaped rather like a crocodile and had an extensive armour around its body.

The first Elgin reptile to be recognized as such was *Leptopleuron lacertinum* Owen 1851 (objective synonym, *Telerpeton elginense* Mantell 1852), based on a small skeleton collected at Spynie (Benton 1983c). Further finds (Huxley 1867; Boulenger 1904; Huene 1912a, 1920) showed it to be a procolophonid, a small omnivorous or herbivorous reptile with a triangular, spiked skull (text-fig. 3E). The skull was about 52 mm long, and the body may have been up to 400 mm in total length.

The third animal to be obtained from the Lossiemouth Sandstone Formation was named *Hyperodapedon* by Huxley (1859a). It was interpreted as a rhynchosaur (Huxley 1869, 1887; Burckhardt 1900; Boulenger 1903; Huene 1929; Benton 1983d, 1984), a group of diapsid reptiles that were abundant in many faunas worldwide in the middle and late Triassic. Its closest relative is *H. huxleyi* from the Maleri Formation of India. *Hyperodapedon* was a bulky 1.3 m long quadruped

TABLE 1. Classification of the reptiles of the Lossiemouth Sandstone Formation.

SUBCLASS ANAPSIDA

Family Procolophonidae Cope 1889

Leptopleuron lacertinum Owen 1851 (objective junior synonym, *Telerpeton elginense* Mantell 1852)

SUBCLASS DIAPSIDA

Cohort Archosauromorpha Huene 1946

Superorder Rhynchosauria Osborn 1903

Family Rhynchosauridae Huxley 1887

Hyperodapedon gordonii Huxley 1859 (subjective junior synonym, *Stenometonon taylori* Boulenger 1903)

Superorder Archosauria Cope 1869

Order Thecodontia Owen 1859

Family Stagonolepididae Lydekker 1887

Stagonolepis robertsoni Agassiz 1844

Family Ornithosuchidae Huene 1908

Ornithosuchus longidens (Huxley 1877) (subjective synonyms, *Dasygnathus longidens* Huxley 1877; *O. woodwardi* Newton 1894; *O. taylori* Broom 1913)

Family Erpetosuchidae Watson 1917

Erpetosuchus granti Newton 1894

Family Scleromochliidae Huene 1914

Scleromochlus taylori Woodward 1907

Order Saurischia Seeley 1888

Family Procompsognathidae Huene 1921

Saltopus elginensis Huene 1910

Cohort Lepidosauromorpha Benton 1983

Superorder Lepidosauria Haeckel 1866

Order Sphenodontia Williston 1925

Family Sphenodontidae Cope 1870(?)

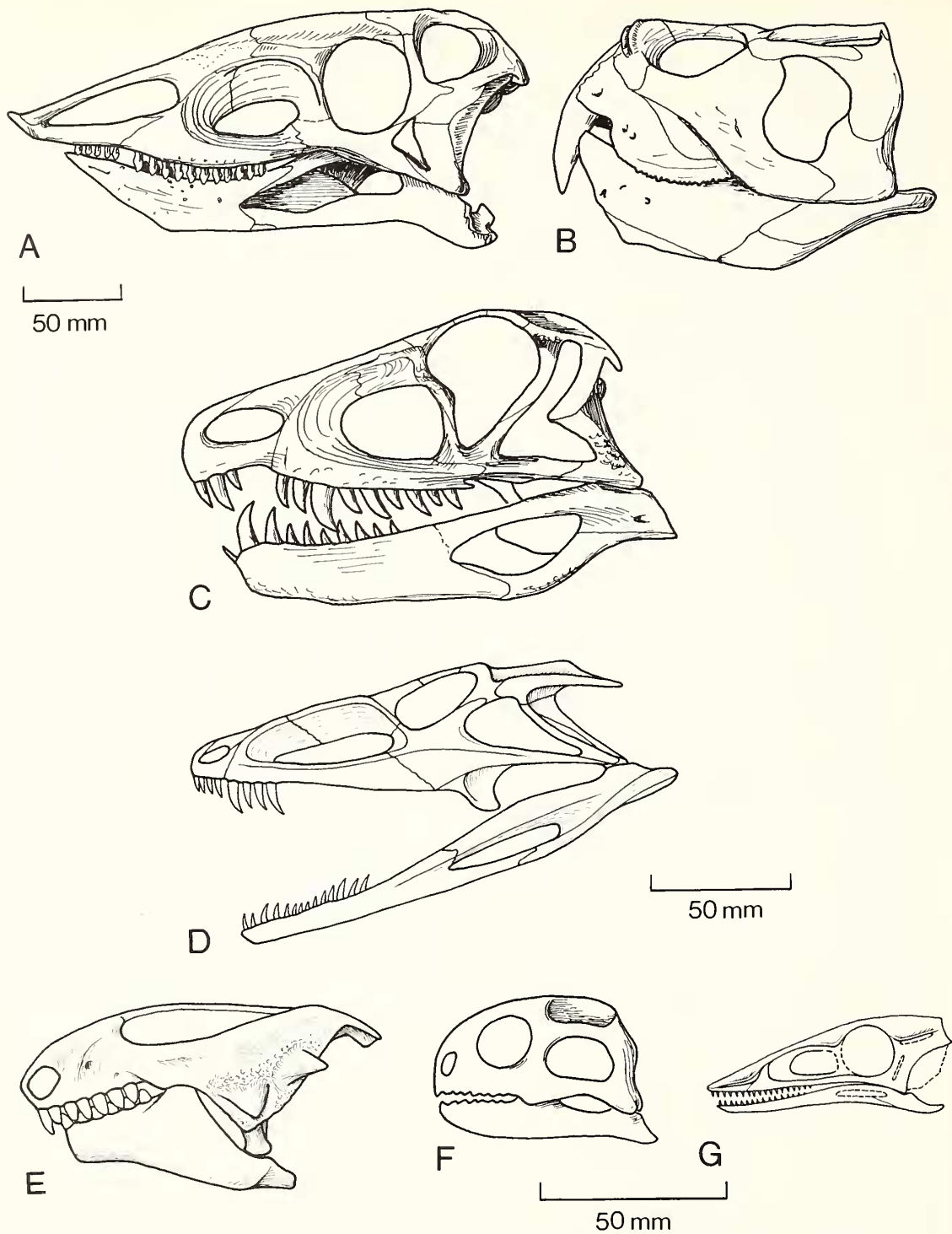
Brachyrhinodon taylori Huene 1910

with strong limbs—the hind-foot had large claws and was probably adapted for scratch digging. The skull was the most remarkable feature (text-fig. 3B). It was 100–200 mm long and very broad at the back—there was an anterior premaxillary ‘beak’ and the teeth were arranged in multiple rows on the maxilla. The dentary had a sharp edge and it cut into a groove in the maxillary toothplate, providing a strong shearing bite.

Remains of the medium-sized carnivore *Ornithosuchus* (text-fig. 3C) were described by Huxley (1877), Newton (1894), Boulenger (1903), Broom (1913), Huene (1914), and Walker (1964). This animal was probably partly quadrupedal and partly bipedal, and it had sharp dagger-like teeth. Several specimens are known and these indicate a range in skull length of 50 to 450 mm and in body length of 0.5–3.5 m. *Ornithosuchus* was regarded by Walker (1964) as an ancestral carnosaur, but comparison with *Riojasuchus* (Bonaparte 1969) suggests that it had a ‘crocodile-reversed’ type of ankle joint (Cruickshank 1979) rather than the mesotarsal joint typical of dinosaurs, and was thus a thecodontian closely related to some South American forms (Bonaparte 1969).

A second small carnivore (or insectivore) is *Erpetosuchus* which was collected from a block built into a wall in Lossiemouth in the early 1890’s (Newton 1894). The specimen includes a skull (text-fig. 3D), the fore-limbs and shoulder girdle, and the armour plates, which indicate a total body length of about 600 mm. It seemed to have some crocodylian characters (Walker 1968), but these were later considered to be the result of convergence. *Erpetosuchus* is another advanced pseudosuchian thecodont with a narrow 75 mm long skull which has a huge antorbital fenestra and a broad ‘square’ posterior skull roof (Walker 1970, pp. 364, 367–368; Krebs 1976, pp. 87–89).

Extensive collecting by William Taylor, a local naturalist, between 1890 and 1920, produced abundant remains of these animals from Lossiemouth and Spynie, as well as the holotypes of three new genera: *Scleromochlus*, *Saltopus*, and *Brachyrhinodon*.



TEXT-FIG. 3. The reptiles of the Lossiemouth Sandstone Formation, near Elgin (late Triassic: early Norian). Skulls of A, *Stagonolepis*; B, *Hyperodapedon*; C, *Ornithosuchus*; D, *Erpetosuchus*; E, *Leptopleuron*; F, *Brachyrhinodon*; and G, *Scleromochlus*, drawn to three different scales (A-C, D, E-G). The skull of *Saltopus* is not known. (A, after Walker 1961; B, after Benton 1983*d*; C, after Walker 1964; D, original; E, original; F, after Huene 1910*b*; G, original.)

Scleromochlus was based on several skeletons which showed an animal with a short body, short forelimbs, but long hindlimbs and long tail (Woodward 1907; Huene 1914). The skull (text-fig. 3G) is relatively large, but very lightly built. Overall body length was about 250 mm. *Scleromochlus* is a fourth thecodontian whose skull specializations suggest a relationship to the aetosaurus (Walker 1970, p. 361; Krebs 1976, p. 90). One specimen (BMNH R3146) shows transverse bands of thin dorsal scutes, figured by Woodward (1907) as abdominal ribs.

Saltopus (text-fig. 6A), represented by only one skeleton, and unfortunately lacking the skull, is Elgin's only dinosaur (Huene 1910a). The vertebrae and limbs are rather poorly preserved in outline, and the total body length was probably about 600 mm. It is a coelurosaur (Walker 1970, p. 359), and may be a podokesaurid (Huene 1914; Steel 1970) or a 'procompsognathid' (Romer 1966).

Brachyrhinodon (text-fig. 3F; Huene 1910b, 1912b) was a small animal 200–250 mm long, with a short snout, acrodont teeth, and teeth on the palate. It was probably an omnivorous sphenodontid related to *Polysphenodon* from the late Triassic of Germany (Walker 1966).

One small undescribed thecodontian is represented by a 'somewhat obscure skeleton in Manchester Museum' (MM L8270; Watson 1909a). This consists of a disarticulated skull, some of the skeleton, and some scutes. It is probably a new form, but is too poor to be described.

The record of a lungfish tooth-plate from Spynie, identified as *Ceratodus* (Traquair 1895, p. 280) is an error. This record is attributed by Taylor (1920) to Huxley, but he gives no reference and we have been unable to find that Huxley mentions it. The earliest reference appears to be that of Judd (1886a). The error was caused by confusion between the Triassic locality 'Spynie' and 'New Spynie' (now called Quarrywood), which lies on Upper Old Red Sandstone 4 km to the west. This was pointed out by Taylor (1920) and has been confirmed by one of us (A.D.W.) from examination of the matrix of the original specimen (EM 1978.348.1A, B) and from the making of casts from it. The tooth-plate is probably of *Phaneropleuron* (T. S. Westoll, pers. comm.) and the locality is most likely Leggat Quarry (NJ 176635), 850 m to the south-west of Quarrywood, as suggested by Taylor (1901, p. 48).

Reptiles from the Rhaetic of Linksfield

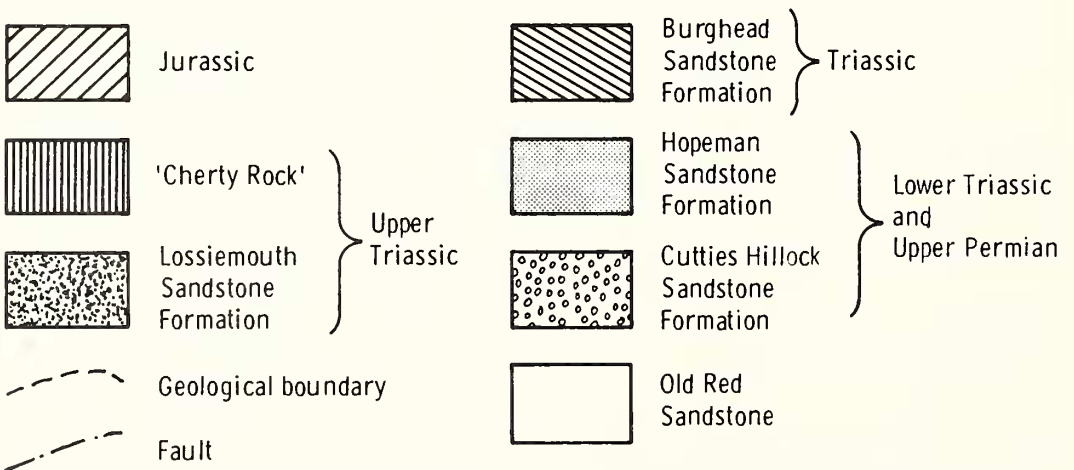
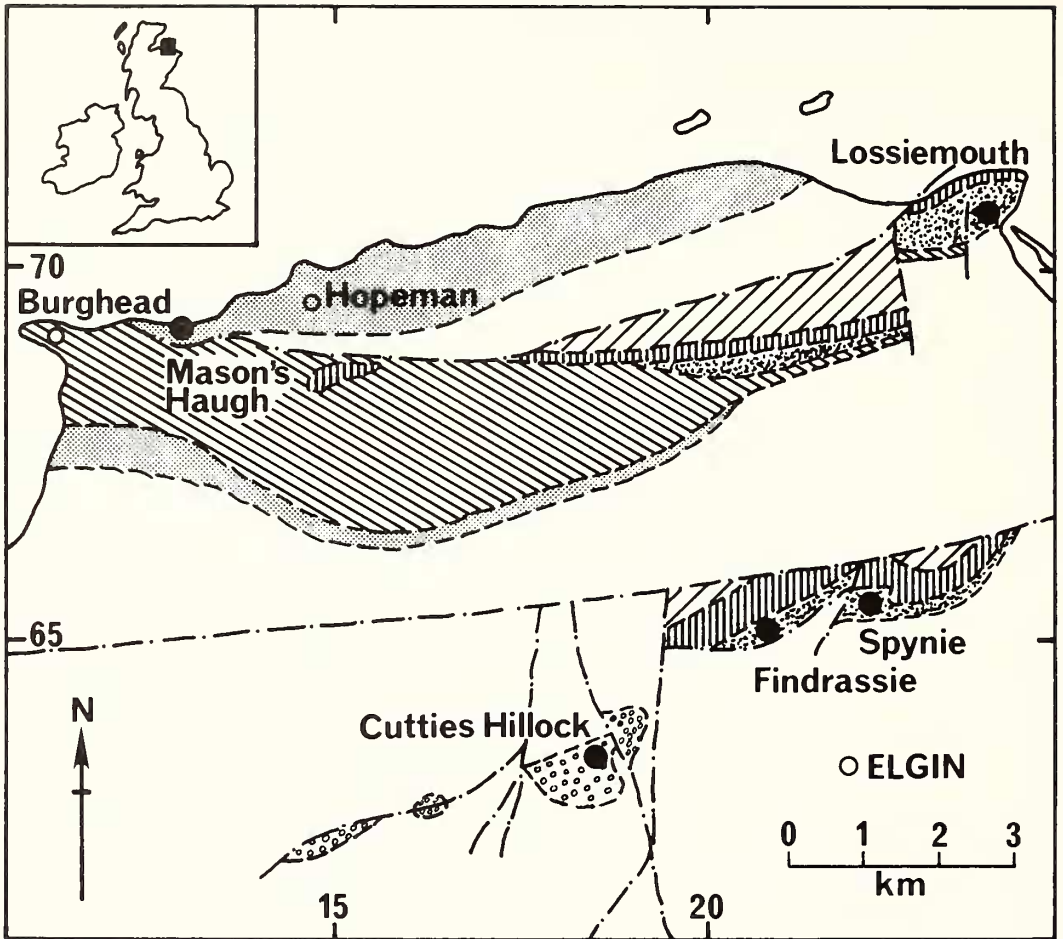
A large glacial erratic at Linksfield, near Elgin (NJ 222641) has yielded some reptile remains, as well as fish. The sediments were originally determined as Purbeck or Wealden (Duff 1842), but they were later dated as Rhaetic (Moore 1860, Jones 1863, Anderson 1964) on the basis of the fish and ostracods. Duff (1842, pl. 4.5) figured spines, scales, and teeth of such fish as *Hybodus*, *Lepidotes*, *Sphenonchus*, and *Acrodus*, as well as a plesiosaur vertebra and teeth, and a femur of a 'chelonian reptile' which Seeley (1891) later described as the femur of a crocodile *Sauroides robertsoni*.

STRATIGRAPHICAL TERMINOLOGY

The Permo-Triassic of the Elgin area outcrops in two belts, one along the coast between Burghead and Lossiemouth, and the other in the region of Elgin itself (text-fig. 4). The beds near Elgin occur in small fault-blocks within petrologically similar Upper Old Red Sandstone.

The nomenclature of the Hopeman and Cutties Hillock sandstones

Formal lithostratigraphical terms for the main units of the Permo-Triassic of the Elgin area were introduced by Warrington *et al.* (1980). The Hopeman Sandstone Formation was proposed to include predominantly aeolian sandstones some 60 m thick cropping out along the coast between Cummingstown and Covesea Skerries Lighthouse, and also for a separate strip of similar rocks, 30–45 m thick, lying on top of the Quarry Wood ridge and in the Knock of Alves area to the west of Elgin. Although there is some evidence which suggests that the sandstones of these two regions are broadly equivalent, and while it is true that the coastal sandstones are much better exposed (although the base is not seen), the combination of these two units is not altogether logical and has other undesirable consequences. The most important of these is that the name 'Cutties Hillock' for a world-famous fossil vertebrate locality and set of beds has disappeared, to be replaced by an unfamiliar



TEXT-FIG. 4. The distribution of the Permo-Triassic beds around Elgin, north-east Scotland. The formations are indicated by shading, and the main reptile and footprint localities are named.

name. Furthermore, apart from a small scrap of bone (Peacock *et al.* 1968, p. 59) the coastal sandstones have yielded nothing but reptilian tracks, whereas the reptilian fauna comes entirely from the inland localities. Thus the accurate determination of the age of this Formation has to be obtained from a study of the reptiles, none of which occurs in the type area.

The tracks from the coastal sandstones are believed to have been made by dicynodont reptiles, but this is a group which ranges in time from the middle of the Permian until late in the Triassic. Hickling (1909) considered that the closest comparisons of these tracks were to be made with those from Mansfield and Penrith. According to Smith *et al.* (1974), the Mansfield Stone is a variety of the Lower Magnesian Limestone and is thus early Upper Permian in age, while the tracks from Penrith are late Lower Permian. In contrast, the Cutties Hillock fauna is probably very late Permian in age (see below). Tracks were also seen at Cutties Hillock Quarry itself in 1878 before the reptiles were discovered (Peacock *et al.* 1968, p. 73) and have occasionally been seen since. A single small print from a nearby quarry, the position of which is now uncertain, was figured by Watson and Hickling in 1914. However, these tracks can surely only be used as evidence of a broad time-equivalence between the sandstones of the two areas.

Glennie and Buller (1983) have suggested that the Hopeman Sandstone on the coast could be divided into two units, a lower one of late Lower Permian age, and an upper one, presumed to be equivalent to the Cutties Hillock beds and thus of latest Permian age. They considered that the contorted sandstones seen in the coastal sections lie at the same stratigraphical horizon and owe their origin to the Zechstein marine transgression. Williams (1973), on the other hand, divided the coastal sandstones into four successive phases, the first three of which terminated in contorted strata (he followed Peacock *et al.* (1968), however, in regarding the coastal and inland strips as time-equivalents).

While we do not agree with the conclusions of Glennie and Buller (1983) concerning the subdivision of the Hopeman Sandstone on the coast, these differences of interpretation serve to underline the necessity for a separate formal lithostratigraphical unit to include the reptile-bearing beds, to avoid confusion, and until such time as definite correlations shall have been established. It is proposed, therefore, that these inland beds be termed the *Cutties Hillock Sandstone Formation*.

Peacock *et al.* (1968) preferred to use the name 'Sandstones of Cutties Hillock (Quarry Wood)' instead of 'Cutties Hillock Sandstone' because 'Cutties Hillock' does not occur on Ordnance Survey maps (it does actually appear on a map by Gordon (1892)). However, this is not a strong objection, since the position of the quarry is given by Judd (1886a, pp. 397-398) and is well established by local tradition. The term 'Cutties Hillock Sandstone Formation' has in fact already been used by Smith *et al.* (1974, p. 25), although not formally defined.

Origin and correct form of the name Cutties Hillock

Although various suggestions have been made, including 'short hillock' and 'witches' hillock', it seems most likely that the name derives from a Gaelic original. It does not seem to have appeared in print until after the discovery of the reptiles in 1884. Mackie, an important worker on the local geology and discoverer of the Rhynie Chert, always used the form 'Cuttieshillock' in several papers (e.g. 1897) and in articles in local newspapers. Other local writers tended to do the same; furthermore, the old labels on the specimens from this locality in Elgin Museum also use this form. Maxwell (1894) mentions, among other similar names, 'Kittyshalloch' in Galloway and 'Cuttyshallow' in Ayrshire. In the last instance he gives the derivation as the Gaelic *ceide sealghe*, pronounced to sound something like 'kedyshalluh' and meaning 'hill-brow of the hunting'. It appears, therefore, that originally the name had nothing to do with the words 'cutty' or 'hillock', but when it was written down, authors tended to split it into two words, transferring the 's' to the first of these and sometimes adding a singular or plural apostrophe as seemed appropriate.

However, in the interests of stability of nomenclature and since writers on the derivation of place-names often disagree strongly with each other, it seems better to rely on first published usage in the scientific literature. This is that of Judd (1885, p. 573), who speaks of the 'Cutties Hillock quarry', and this usage, omitting the apostrophe, is by far the most common in the literature.

Cutties Hillock Sandstone Formation

Type area. Quarries and natural exposures on Quarry Wood ridge, the Knock of Alves and Carden Hill west of Elgin. The formation is seen to rest unconformably on Rosebrae Beds of the Upper Old Red Sandstone in Rosebrae Quarry (NJ 173633) and York Tower Quarry (NJ 162629). The reptile fauna comes mainly from Cutties Hillock Quarry (NJ 185638).

The classification of the Elgin Permo-Triassic

The classification of the Permo-Triassic rocks around Elgin, using the new terminology (Warrington *et al.* 1980), and as recommended here, is:

- Cherty Rock (??Norian–Rhaetian)
 Lossiemouth Sandstone Formation (Carnian–Norian)
 (Synonyms: Reptiliferous Sandstone (pars) (Symonds 1860; Harkness 1864; Judd 1873, 1886*a*, *b*; Gordon 1892; Traquair 1895; Mackie 1897; Boulenger 1903); Elgin Sandstone (Newton 1894); *Stagonolepis* Beds (Boulenger 1904; Huene 1910*a*); *Stagonolepis* Sandstone (Watson 1909*b*; Huene 1910*b*, 1912*a*, *b*, 1913, 1914); Sandstones of Lossiemouth, Spynie, and Findrassie (Westoll 1951); Sandstones of Spynie, Lossiemouth, and Findrassie (Peacock *et al.* 1968)).
- Burghead Sandstone Formation (??Anisian–Carnian)
 (Synonyms: Burghead Sandstones (Westoll 1951); Burghead Beds (Peacock *et al.* 1968)).
- Hopeman Sandstone Formation (Late Permian)
 (Synonyms: Sandstones of Cummingstone (Huxley 1859*b*, 1877); Cummingstone Beds (Hickling 1909; Watson 1909*b*; Watson and Hickling 1914); Reptiliferous Sandstone (pars) (Symonds 1860; Harkness 1864; Judd 1873, 1886*a*, *b*; Traquair 1895); Sandstones of Cutties Hillock and Hopeman–Cummingstone (pars) (Westoll 1951); Sandstones of Cuttie Hillock (Quarry Wood) and Hopeman (pars) (Peacock *et al.* 1968)).
- Cutties Hillock Sandstone Formation (Late Permian)
 Reptiliferous Sandstone (pars) (Judd 1886*a*, *b*; Traquair 1895; Mackie 1897); Elgin Sandstone (Gordon 1892; Newton 1893); Cutties Hillock Beds (Watson 1909*b*); *Gordonia* Beds (Boulenger 1904); *Gordonia* Sandstone (Huene 1913); Sandstones of Cutties Hillock and Hopeman–Cummingtown (pars) (Westoll 1951); Sandstones of Cutties Hillock (Quarry Wood) and Hopeman (pars) (Peacock *et al.* 1968); Cuttie's Hillock Sandstone (Walker 1973)).

OCCURRENCE OF THE REPTILES

Sedimentology of the Hopeman Sandstone Formation (s.s.)

The Hopeman Sandstone Formation of the coast between Cummingstown and Covesea Skerries and Halliman Skerries, some 60 m thick, shows evidence of largely aeolian deposition: large-scale cross-bedding is common, and the sandstones are generally composed of well-rounded grains of quartz and feldspar, often of high sphericity, with only a little mica (Peacock *et al.* 1968, p. 59). However, the action of water is indicated in places by lenses of coarse sandstone and well-rounded pebbles with small-scale cross-bedding, as well as contorted beds (Peacock 1966). Williams (1973) identified four phases of dunes: seif dunes at the base, followed by three phases of barchan dunes. Each of the first three phases is topped by contorted beds and sheet flood or playa lake deposits. The fossil tracks have been obtained principally from Masonshaugh Quarry, Cummingstown (NJ 125692). Occasional footprints have been observed in Greenbrae Quarry (NJ 137692) and Clashach Quarry (NJ 163702), and Peacock *et al.* (1968, p. 59) report an unidentifiable bone fragment from Greenbrae.

Taphonomy of the Hopeman Sandstone Formation footprints

The footprints of the Hopeman Sandstone Formation may be preserved on low-angle dune foresets, but this has only been observed in a few *in situ* occurrences. The slabs collected in the nineteenth century may include some from horizontal bedding planes. However, there is usually a mound of sand behind each print (Brickenden 1852; Huene 1913; Watson and Hickling 1914), and this would

suggest that the animals were moving uphill. These mounds are seen also behind the large footprints at Clashach (text-fig. 1c).

Martin (c. 1860) gave a detailed account of the occurrence of tracks at Masonshaugh, and notes that they were all heading in one direction (towards today's North Pole). He considered that the producers were moving down to the Moray Firth across the beach to feed in the sea! The Elgin footprints may be interpreted as individual trackways formed by two or three species of mammal-like reptiles, each displaying a range of sizes, heading across a dune-field towards the centre of the depositional basin to the north.

Sedimentology of the Cutties Hillock Sandstone Formation

The Cutties Hillock Sandstone Formation is between 30 and 45 m thick. It may be divided into two units (Peacock *et al.* 1968; Williams 1973): a lower phase (up to 4 m thick) consisting of a series of pebbly sandstones that lie discordantly on the Old Red Sandstone, and an upper phase which consists of about 30 m of large-scale light brown and yellow cross-bedded sandstone. The lower pebbly beds have been interpreted as sheet flood deposits, but the presence of dreikanter pebbles with rounded edges suggests that they were exposed to wind erosion before being reworked by water (Mackie 1902; Watson 1909*b*; Watson and Hickling 1914; Williams 1973). The upper phase shows well-rounded quartz grains and unidirectional foresets which indicate fossil barchan dunes. The reptiles *Elginia*, *Gordonia*, and *Geikia* came from Cutties Hillock Millstone Quarry (NJ 185638) and an isolated footprint and other trackways were found nearby (Linn 1886; Huene 1913; Watson and Hickling 1914). Walker (1973) found an un-named dicynodont in York Tower Quarry, Knock of Alves (NJ 162629). An unidentified bone in Forres Museum was found in Crownhead Quarry (NJ 183630) on the south side of Quarry Wood hill and is of interest as the only bone recorded from this part of the outcrop. A slab in Elgin Museum showing footprints with a tail-drag on top of ripple-marks probably came from 'Robbies Quarry', the position of which is uncertain, but it was probably one of the Crownhead group of quarries.

Taphonomy of the Cutties Hillock Sandstone Formation reptiles

The reptiles from the Cutties Hillock Sandstone Formation appear to have been collected from the base of the upper phase, just above the pebbly sandstones. Judd (1886*a*, pp. 400–401) noted that 20 feet (6.2 m) of the 'Reptiliferous Sandstone' was to be seen above the pebbly layers, and that the remains of five reptiles all came from one horizon and that a sixth came from the bed below. Phillips (1886) confirmed this. Gordon (1892, p. 242) referred to 'a portion of this conglomerate containing reptilian remains'. Newton (1893, pp. 462, 466) also noted that the specimens of *Gordonia juddiana* and *Geikia elginensis* contained pebbles in the matrix like those of the 'conglomerate' bed. There are also pebbles in the specimen of *Gordonia duffiana*. These blocks (EM 1978.559.1, 2) show quartz pebbles up to 20 mm and up to 7 mm in diameter respectively.

The skeletons are well articulated, and some show series of vertebrae, ribs, and limbs with the skull in position. The type of *Elginia* (GSE 4783–4788) lacks its lower jaws. Details of the association of parts have been lost in some specimens, however, because only parts were collected and sufficient care was not exercised in keeping associated blocks together. The animals are preserved generally on their sides, although one pelvis (RSM 1966.42.3) is spread out flat. *G. duffiana* (EM 1978.559.1, 2), however, has the vertebrae and some limb bones passing vertically into the plane of bedding. In general, the 'long' skulls appear to be preserved on their sides, and the 'wide' skulls lie flat with the skull roof parallel to the plane of bedding, or in a vertical 'nose down' attitude (e.g. RSM 1956.8.3).

Individual bones may be distorted. The bones are represented by cavities in the rock from which virtually all bone material has disappeared, and the interface with the sandstone may be stained with black material containing iron, manganese, and cobalt (Newton 1893, p. 435). The cavities may be compressed with opposite impressions almost touching. Limb bones may be particularly flattened, and the ends may be hard to interpret either because of poor preservation and compression, or because the ends were largely cartilaginous in life. The centra of the dicynodont vertebrae are usually missing or very poorly preserved, although neural arches and ribs may be easy to cast. By contrast,

the centra of *Elginia* are well preserved. Skulls are often vertically compressed (Newton 1893; Walker 1973; Rowe 1980), and in *G. duffiana* most of the squamosals and the right half of the occiput are missing, which presumably indicates post-mortem, pre-fossilization damage.

Sedimentology of the Lossiemouth Sandstone Formation

The Lossiemouth Sandstone Formation is distributed in several small fault-bounded blocks at Lossiemouth, Spynie, and Findrassie (Peacock *et al.* 1968, pp. 67–69; Williams 1973). The thickness of the unit varies from 7 to 30 m. It is underlain by strata which have been interpreted as a thin representative of the Burghead Sandstone Formation. Peacock *et al.* (1968) suggested that the Burghead Sandstones (mainly point bars in their type area, according to Williams (1973)) interdigitate with the Lossiemouth Sandstones to the west and, following Westoll (*in Watson et al.* 1948), they interpreted the thin calcareous sandstones below the typical Lossiemouth Sandstone Formation at Lossiemouth as a reduced lateral equivalent of the Burghead Sandstone Formation. However, this interpretation is hard to prove because there is a large geographic gap between the outcrops of typical Burghead and typical Lossiemouth beds, and because we have no information on what succeeds the Burghead Sandstones in their type area. The Lossiemouth Sandstone Formation is overlain by the Cherty Rock (sandy limestone and chert).

The Lossiemouth Sandstones are white, buff, yellow, or pinkish. Grain size is usually uniform (0.2–0.5 mm) with grains well-rounded. The rock is composed of quartz, feldspar, and rare brownish chert and quartzite. Cements are usually overgrowths of secondary quartz and feldspar, but calcite and fluorspar may also occur (Peacock *et al.* 1968, pp. 69–70).

The sandstones may be finely laminated, but more usually they show large-scale cross-beds on well-weathered surfaces. These features, as well as the absence of pebbles, the rarity of micas and heavy minerals, strongly suggest aeolian deposition.

Foreset analysis of the cross-beds indicates a prevailing south westerly wind forming barchan dunes. These have been interpreted (Williams 1973, pp. 132–135) as reworked sand from the underlying Burghead Sandstone Formation, which he regards as composed of flood-plain sandstones at Lossiemouth. Dunes up to 20 m high migrated across the flood plain during arid periods, and the aeolian deposition was terminated by large-scale flooding and the deposition of silicified and calcareous sandstone ('Sago Pudding Sandstone', Peacock *et al.* 1968, p. 71; Williams 1973, pp. 136–143; upper part of Lossiemouth Sandstone Formation).

The reptiles were obtained from Lossiemouth East Quarry (NJ 236707), Lossiemouth West Quarry (NJ 231704), Spynie (NJ 223657, and others), and Findrassie (NJ 202650?). Taylor (1920) reported a specimen of *Leptopleuron* (EM 1920.5) from a glacial erratic of Triassic beds on the Hill of Meft, north-west of Urquhart (NJ 268642).

Taphonomy of the Lossiemouth Sandstone Formation reptiles

The skeletons of *Stagonolepis* and *Hyperodapedon* were apparently found just above the base of the Lossiemouth Sandstone Formation. Murchison (1859, p. 428) stated that the bones found then were collected 'in the lowest part' of the freestones being quarried at Lossiemouth. Gordon (1859, p. 46) confirmed this, stating that the lowest beds at Lossiemouth were red clay, succeeded by yellowish soft sandstone and then harder sandstone. The red clay may be equivalent to that reported by Peacock *et al.* (1968, p. 65) as 'micaceous siltstone', the yellowish soft sandstone may be the 'Burghead Beds equivalent', and the harder sandstone is probably the Lossiemouth Sandstone Formation. The bones were found 'immediately under this hard siliceous sandstone in a quarry half-way to the new harbour from Rockhouse, and in the face of the wall of rock that overhangs the houses fronting the old harbour . . .'. This refers to the east end of Lossiemouth East Quarry (NJ 237707). Judd (1873, p. 137) stated that the reptiles were found '100 ft. below the top of the sandstones', which would imply about the base of the Lossiemouth Sandstone Formation, if its complete thickness is taken into account. Judd (1886a, pp. 397, 403) added that the reptile remains all came from 'a single band of soft rock'. Further, Gordon (1892, p. 245) suggested that 'if any excavation were to be made for fossils alone, it should be, in the first place, in the Lossiemouth quarries, and in the platform left by the quarrymen.

They did not go further down, because the bed was softish and rubbly, but it was at this horizon more than elsewhere in the quarry that most fossils were found.'

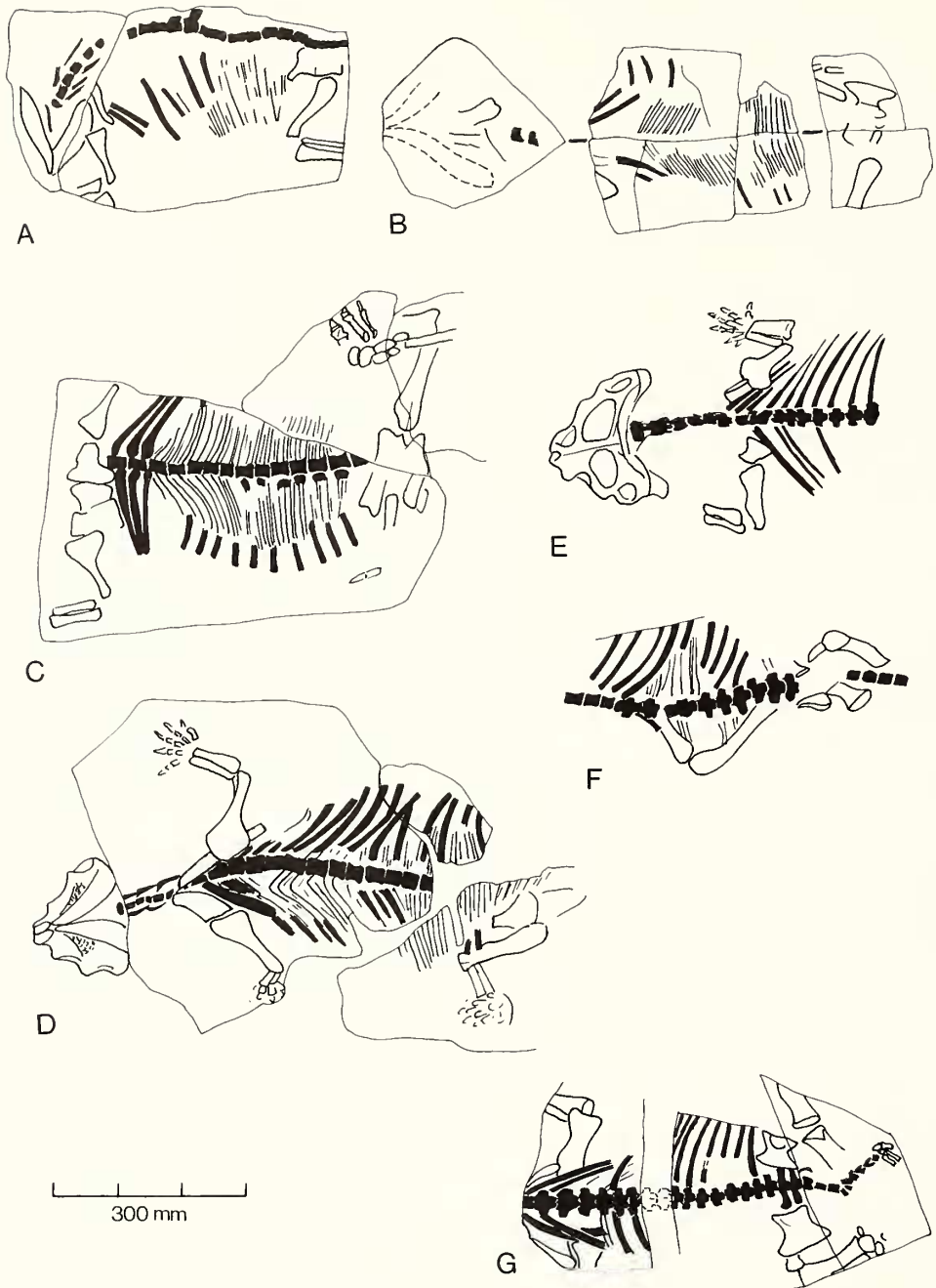
At Spynie the reptiles also appear to have been found low in the Lossiemouth Sandstone Formation. The type specimen of *L. lacertinum* 'was found by Mr. William Young at the bottom of a shaft which had been sunk through 51 feet of sandstone down to a soft rubbly bed' (Duff *in* Murchison 1859, p. 435). Gordon (1859, pp. 45–46) added that the specimen was 'extracted from the living rock, deep in a quarry opened on the west end of the hill' and Martin (*c.* 1860) stated that the specimen was 'found low down, in the bottom of the quarry'. The quarry has been identified as an old pit at NJ 2206 6557 (Peacock *et al.* 1968, p. 68). *Hyperodapedon* apparently came from another pit nearby: 'the most westerly of the Spynie quarries' (NJ 2192 6555) (Gordon *in* Huxley 1877; Linn 1886; Peacock *et al.* 1968, p. 68). These openings were probably abandoned over 100 years ago, judging by the large trees growing in them, and *Ornithosuchus*, collected in 1891, may have come from the large quarry still in operation (NJ 2225 6565). This was the site of two fine skulls of *Hyperodapedon* collected in about 1948 (now in RSM).

The first finds of *Stagonolepis* from Findrassie were made 'near the east entrance to Findrassie House, and among the debris of a pit opened up for road material' (Gordon 1859, p. 44). The East Lodge of the Findrassie Estate is situated at NJ 2074 6545, and the pit could be one of the remaining Findrassie quarries which lie south and south-west of the entrance (Peacock *et al.* 1968, p. 69), or it could have been filled (Walker 1961, p. 106). On the original geological survey of the Elgin area, Linn (1886) recorded that *Stagonolepis* was found 'in the more westerly' of a line of three quarries (?NJ 2015 6495). Peacock *et al.* (1968, p. 137) suggest a more easterly pit at NJ 205651 as the source of the reptiles. Most of the Findrassie specimens figured by Huxley (1877) are in the form of well-preserved moulds. However, some specimens in Elgin Museum labelled 'Findrassie' look different and have bone preserved—this may indicate a different locality. There are occasional pebbles in the matrix, and the early specimens at least occurred at the base of the reptiliferous sandstone, just above the Upper Old Red Sandstone (Gordon 1859; Walker 1961).

Unfortunately, in no case is it clear what relationship the skeletons bore to the ancient dunes. Some of the *Stagonolepis* slabs from Lossiemouth in the RSM show cross-bedding and slightly more mica than usual on the base. The aeolian foreset cross-bedding is generally only visible in the lower parts of the Lossiemouth Sandstone Formation, because of extensive silicification higher up (Williams 1973). This again confirms the suggestion that most of the reptile specimens came from near the base of the formation. There is very little mica in typical Lossiemouth Sandstones, but there is up to 6% of total composition in the underlying flood plain deposits, and small amounts also in the overlying Sago Pudding Sandstone.

Outline sketches of the more complete skeletons of *Hyperodapedon* (text-fig. 5) show that most were fossilized flattened in a horizontal plane, although it is hard to say whether they are lying on their bellies or on their backs. Only the type specimen lies partially on its side (text-fig. 5A). The vertebral column is usually unbroken and the ribs and gastralia retain their associations. The limbs are often in a natural resting pose, with the forelimbs flexed and pointing forwards, the hindlimbs pointing forwards or backwards. The shoulder girdle and pelvis may retain their original positions, but they usually collapse. The skull is often present undamaged and in close articulation with the vertebral column. In these specimens there is no evidence of disarticulation by water currents, wind, or moving sand. The animals generally appear to have died naturally and to have been covered by sand fairly rapidly. One or two isolated bones, such as tooth-bearing elements (EM 1926.6; BMNH R3151, R4780; MM L8272), show that some skeletons were broken up before fossilization.

The remains of the other medium-sized reptiles, *Stagonolepis* and *Ornithosuchus*, are also generally preserved with vertebrae, limbs, and skull in articulation. Even the double row of dermal scutes above the vertebrae of *Ornithosuchus* often occurs in its original position. However, scutes of *Stagonolepis* are very often found isolated, and small bones may be slightly scattered in some cases (e.g. foot of *Ornithosuchus*: Walker 1964, p. 95). The type specimen of *O. woodwardi* (BMNH R2409–2410) is preserved with the skeleton lying on its side and the skull in a horizontal plane. The head is turned back close to the sacrum presumably by drying out of the neck ligaments after death. The



TEXT-FIG. 5. Skeletons of *Hyperodapedon* as preserved to show typical positions of fossilization. Vertebrae and ribs are shaded black, and all other elements are shown in outline. A, EM 1978.566.1-2; B, EM 1978.567.1-3; C, EM 1886.3 (dorsal slab); D, BMNH R699 (dorsal slab); E, BMNH R4782 (from casts); F, BMNH R4791/4805 (from casts); G, RSM 1967.10.1 (from casts).

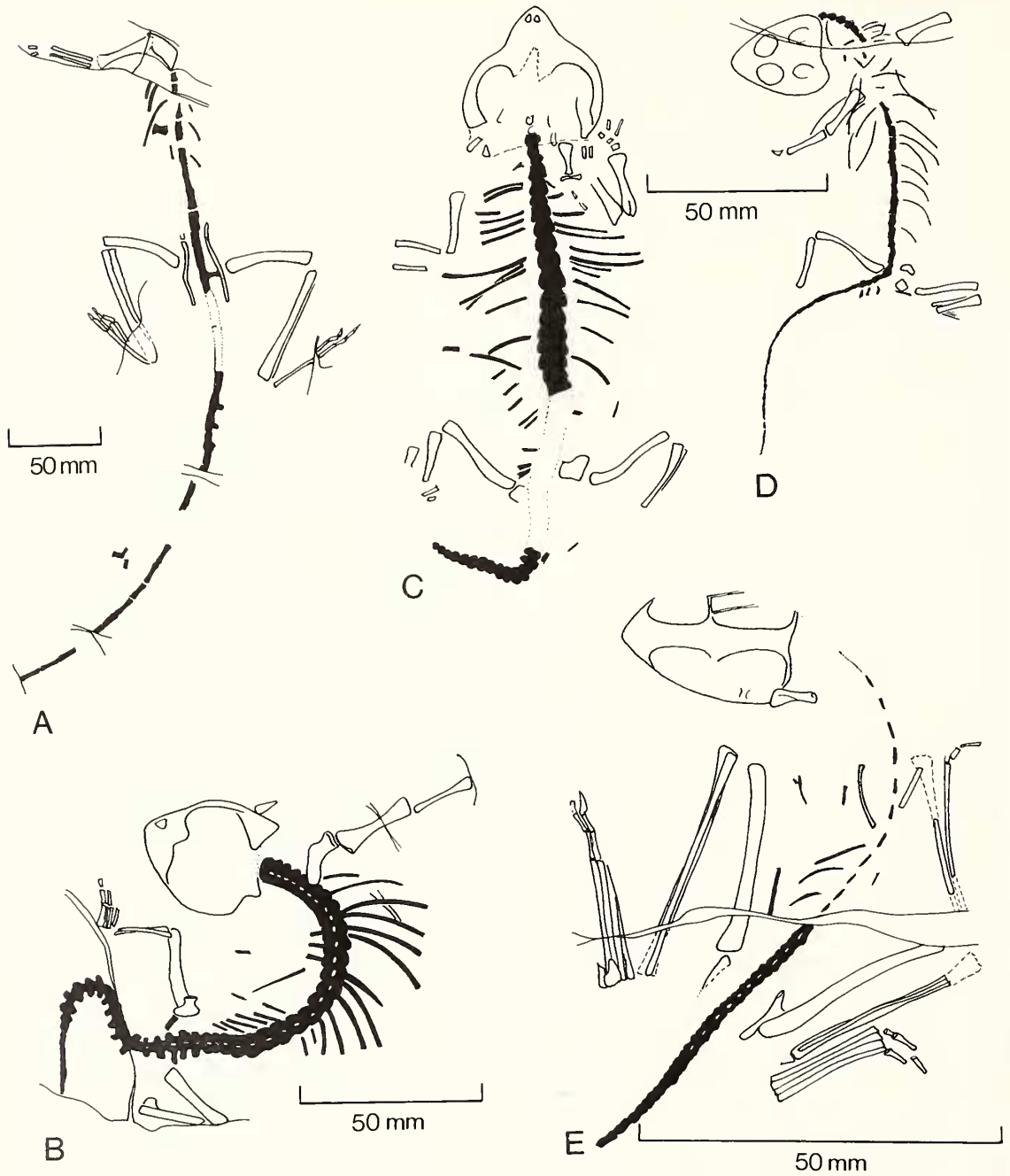
Ornithosuchus skull, BMNH R3143, is preserved on its side. However, it should be stressed that there are no complete specimens available of *Stagonolepis* or *Ornithosuchus*. In fact, only a few specimens of *Stagonolepis* show more than a small group of associated bones, and it is clearly not possible to say a great deal about the attitude and completeness of the specimens. The main reasons for the lack of complete specimens were that there was usually no one with sufficient professional interest around at the time of discovery to make sure that everything was picked up, and it was clearly difficult to collect large fossils which were preserved as moulds in a virtually structureless sediment. This is particularly true of *Stagonolepis* which also had hundreds of scutes around its body: these would have made careful collection even more difficult. Many scutes were doubtless removed from their proper association because they made attractive specimens on their own. Only specimens of *Stagonolepis* and *Ornithosuchus* from Findrassie show signs of transport. They are disarticulated and slightly damaged, and Walker (1961, p. 106) noted that pebbles are occasionally present in the Findrassie matrix. These facts may indicate some reworking by water.

The small reptiles of the Lossiemouth Sandstone Formation (*Leptopleuron*, *Scleromochlus*, *Saltopus*, *Brachyrhinodon*) are often preserved in an undisturbed well-articulated state and flattened in a horizontal plane (text-fig. 6). The skull is in place, the backbone may be straight or curved, and the limbs are in a natural squatting pose, as with the specimens of *Hyperodapedon*. However, there are about ten partial skulls of *Leptopleuron*—isolated mandibles, maxillae, parts of the cheek region. In one specimen the skull roof behind the orbits has been lost, and probably also the upper part of the braincase. One *Brachyrhinodon* has also lost the skull roof. The type specimen of *Erpetosuchus* (BMNH R3139) has the jaws wide open and the forelimbs in a 'standing' pose. Two individuals of *Scleromochlus* are preserved together on one slab (BMNH R3146) with the head of one lying partly over the anterior trunk of the other.

In detail most bones are excellently preserved and they show little sign of crushing or compression. Larger limb bones, however, are more likely to be crushed or distorted, even in association with other unaffected elements. A right ilium (BMNH R4788) and a posterior caudal vertebra (GSM 90884) of *Stagonolepis* became distorted without fracturing, and this led to problems of identification (Walker 1961, pp. 106–107). A skull of *Ornithosuchus* (BMNH R3142) was compressed in such a way that the orbit was reduced to half its original height, and the jugal was distorted (Walker 1964, pp. 58–61). The shoulder girdles of two specimens of *Hyperodapedon* (BMNH R4782; RSM 1967.10.1A) are rather compressed (text-fig. 7A, B), and the skull of BMNH R4782 has also collapsed slightly. The compression of all of these bones has probably been caused by the weight of superincumbent sediment, unusual in a sandstone matrix. Delicate skulls, like those of *Scleromochlus*, may be completely flattened. Various specimens of *Hyperodapedon* (e.g. BMNH R4782; RSM 1967.10.1A, 2; GSM 90932/5) show fine cracks or larger fractures on the surface of the bone (text-fig. 7C) which may be connected with the same process. The cracks have not opened in any way, and they are probably not sun cracks.

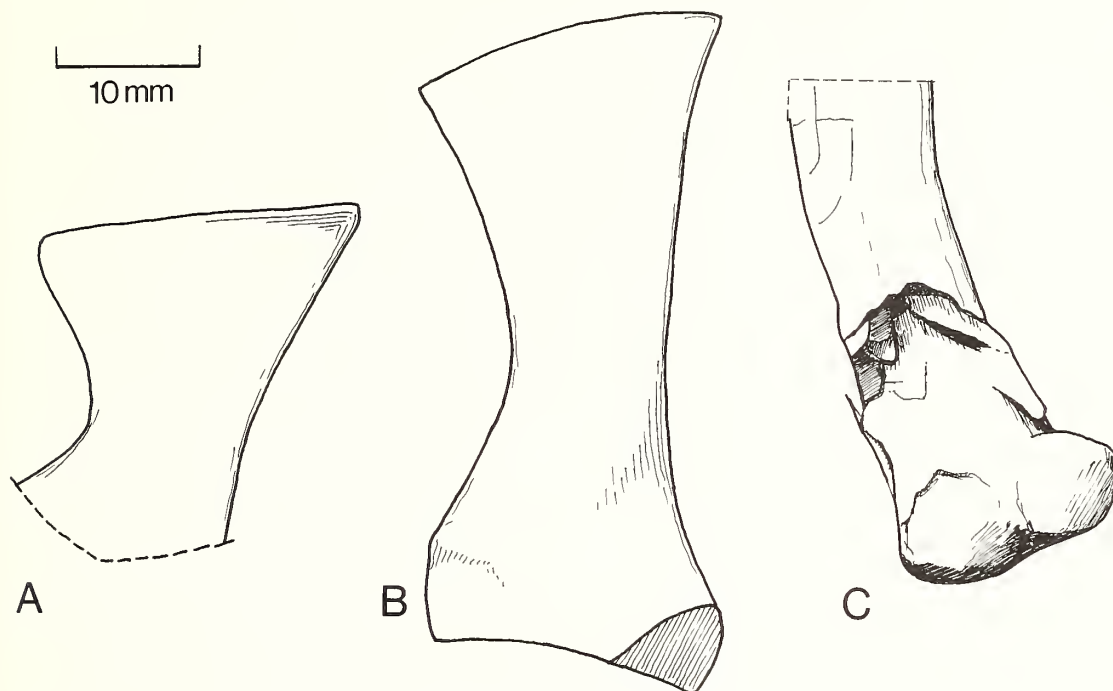
Signs of predation or scavenging appear to be rare, but this is hard to assess because of collection failure in many cases. Walker (1964, pp. 129–131) described a specimen of *Ornithosuchus* (BMNH R3562) in which an articulated skeleton of a large individual has been crushed and broken in certain areas. The anterior scutes of the left side are damaged, the transverse processes of the associated vertebrae are broken off short, the anterior edge of the left scapula, which lies immediately below these vertebrae, is also broken and incomplete. The humerus is broken at the same point and the ribs of the left side are missing. The body has been considerably disturbed in the region of the left shoulder and side, but the rest of the skeleton is not affected, so that the damage was almost certainly caused by a predator or scavenger.

Two isolated skulls of *Hyperodapedon* (RSM. GY.1984.20.1, 2) show similar localized damage. In one the parietal is broken off just behind the attachment of the epipterygoids, and small displaced bone chips are preserved, and the top of the braincase is slightly crushed. This damage occurred before fossilization and probably at, or after, death since the breaks are clean, but there are no tooth or claw marks on the bone. The damage was probably not caused by physical processes since fine sclerotic plates are preserved, only slightly displaced, in the orbit. In the other specimen the braincase



TEXT-FIG. 6. Skeletons of some smaller reptiles from the Lossiemouth Sandstone Formation to show the positions of fossilization. Vertebrae and ribs are shaded black, and all other elements are shown in outline. A, *Saltopus*, BMNH R3915 (ventral slabs); B, *Leptopleuron*, EM 1978.718 (from casts); C, *Leptopleuron*, EM 1920.5 (from casts); D, *Brachyrhinodon*, BMNH R4776 (dorsal slab); E, *Scleromochlus*, BMNH R3556 (from casts).

has been completely removed, and it is represented by only two fractured, displaced bone slivers. The atlas, axis, and two anterior cervical vertebrae are preserved in articulation, but pushed in between the quadrates. Ossified hyoid elements are preserved in place, so the disarticulation is unlikely to have been caused by sedimentary processes.



TEXT-FIG. 7. Compression and pre-fossilization damage to bones of *Hyperodapedon* from the Lossiemouth Sandstone Formation. A, lateral view of a distorted partial left scapula, BMNH R4782 (cast), compared with B, lateral view of a left scapula, restored from casts of EM 1886.3 and BMNH R4795, both from animals of similar size; C, crushed distal end of a femur (cast of GSM 90932/5), showing pre-fossilization damage.

The bone material is either absent (some Findrassie specimens), or very soft and sometimes partly replaced by iron oxide (goethite) and fluorite (Spynie, Lossiemouth). When original material is preserved the structure of bones and teeth may be extremely clear, and the cavities highlighted by the replacement minerals. However, the bones are often preserved as natural moulds in very well-cemented sandstone. Positive preparation has proved to be difficult in most cases, although it has yielded useful information in the study of some specimens of *Stagonolepis* and *Ornithosuchus*. Normally, casts have been made from the natural moulds left as cavities in the rock, and various methods that involve flexible synthetic 'rubbers' have been developed in order to preserve the rock mould and produce a high-fidelity copy of the bone (Walker 1961, 1964, 1973; Benton and Walker 1981).

ECOLOGY OF THE LOSSIEMOUTH SANDSTONE FAUNA (text-fig. 8)

The composition of the fauna of the Lossiemouth Sandstone Formation and the average sizes of its constituents are summarized in Table 2. The absence of plants, invertebrates, and fish, and the relatively small numbers of specimens make it futile to draw up food-chains and calculate biomass and productivity.

Stagonolepis and *Hyperodapedou* dominate the fauna as medium-sized herbivores that must have fed in relatively well-vegetated and watered areas distinct from the dune-fields in which they are preserved. *Stagonolepis* had strong dorsal and ventral armour and a heavy tail. It may have grubbed for plants or invertebrates with its shovel-like snout, and masticated them with its small pointed teeth by means of a slicing jaw action. The structure of the forelimb and shoulder girdle show that *Stagonolepis* normally walked on all fours, and the forelimb may have been used for digging also. For fast movement it may have been able to hold its limbs under the body for short periods, as in crocodiles. *Stagonolepis* was a thoroughly terrestrial animal (Walker 1961).

TABLE 2. The Lossiemouth Sandstone Formation fauna: composition. Information from Walker (1961, 1964), Benton (1977, 1983*d*), and original. Material is listed in the Appendix.

	Body length	Approx. number of individuals
Herbivores		
<i>Stagonolepis</i>	2.1-2.7 m	30(+)
<i>Hyperodapedou</i>	1.0-1.5 m	35
Carnivores		
<i>Ornithosuchus</i>	1.0-3.7 m	12
<i>Saltopus</i>	600 mm	1
Carnivore/insectivore		
<i>Erpetosuchus</i>	?700 mm	2/3
Small omnivores		
<i>Leptopleuron</i>	110-250 mm	?30
<i>Brachyrhinodon</i>	150 mm	?11
<i>Scleromochlus</i>	200 mm	7
		128

Hyperodapedou was a shorter more bulky terrestrial reptile which had powerful limbs. The massive laterally flattened claws of the foot and the construction of the hindlimb strongly suggest that it was used for scratch-digging. *Hyperodapedou* may have fed on buried roots and tubers and other low-level vegetation which it raked up with its premaxillary beak and manipulated with a large tongue. The jaws operated like a penknife, with the dentary cutting into a deep groove on the maxilla. There were multiple rows of teeth that were not replaced from below. There were massive spaces for adductor muscles at the back of the skull, and *Hyperodapedou* probably cut up tough plant material with a powerful precision-shear bite (Benton 1983*b, d*, 1984).

Stagonolepis and *Hyperodapedou* were probably preyed upon, or their carcasses scavenged, by large *Ornithosuchus*. *Ornithosuchus* may have been capable of bipedal locomotion for short spells, as well as quadrupedal locomotion. The long, curved teeth were clearly those of a carnivore, and the spinose scutes along the back may have been necessary for protection against cannibalistic attack (Walker 1964, 1977).

Erpetosuchus was a rare small carnivore and/or insectivore. The dentition was peculiar, with long sharp recurved teeth at the front of the jaws and toothless longitudinal ridges behind which may have been used for crushing the prey. There was also an incipient secondary palate, which may have been connected with the need to masticate the food.

Saltopus, Elgin's only dinosaur, was a small presumably carnivorous coelurosaur. It is more primitive than Huene (1910*a*) indicated, having three rather than four sacral vertebrae, and the anterior blade of the ilium is not very long. Further, *Saltopus* shows no particular adaptations to hopping, as he suggested. Huene also suggested that it had elongate cervical vertebrae, but these are not preserved: the anterior portion and the skull of the only skeleton is missing.



TEXT-FIG. 8. A scene at Elgin, north-east Scotland, in Lössiemouth Sandstone Formation times showing reconstructions of the reptiles in an imaginary scene with typical late Triassic plants. Three *Hyperodapedon* feed on seed-ferns in the foreground. Behind them an *Ornithosuchus* runs towards the armoured *Stagonolepis* which is looking over its shoulder. Behind *Stagonolepis* two *Erpetosuchus* feed on a small carcass. On the rocks in the left foreground are two *Leptopleuron*, a tiny *Brachytrinionon*, and a small bipedal dinosaur, *Saltopus*. To the right of the rocks is the tiny *Scleromochilus* on the side of the pond. In and around the pond there are horsetails, cycads, and ferns, and there are tall lycopods in the distance. Based on a colour painting by Jenny Halstead in Benton (1983*b*).

Saltopus, small individuals of *Ornithosuchus*, and possibly *Erpetosuchus*, probably fed on the small herbivores of the Lossiemouth Sandstone Formation: *Leptopleuron*, *Brachyrhinodon*, and *Scleromochlus*. *Leptopleuron* may be seen as a 'reptilian rodent'. It had transversely broad back teeth consisting of two cusps linked by a narrow cross ridge, that were probably used for grinding up and chopping tough plants sliced off by its sharp, chisel-like front teeth. The teeth were set well forward in the jaws, the lower jaw was deep with a strong (coronoid) process, and the temporal area of the skull was broad, all of which suggests a very powerful jaw closing action. The back of the skull was spiny which may have acted to deter predators, to break up the outline of the animal against a background of spiny vegetation, and/or to form part of an interspecific combat display. The size and form of *Leptopleuron*, and its inferred habitat, are reminiscent of two desert-dwelling lizards: the Coast horned lizard, *Phrynosoma cornutum* from North America, and the Moloch, *Moloch horridus* from Australia.

Brachyrhinodon, a tiny sphenodontid with acrodont teeth on the jaw margins and on the palate, and a very short snout, was probably also a herbivore that could chop up tough vegetation with ease. It was much smaller than the living *Sphenodon* (*Brachyrhinodon* had a skull length of 20–30 mm; *Sphenodon* has a 70 mm skull), and its habits need not have been the same.

Scleromochlus is equipped with long hindlimbs that have been interpreted (Woodward 1907; Huene 1914) as adaptations to jumping, and it may have sought its food on the dunes in which it is preserved. Jumping animals (saltators) have lengthened hindlimbs, the distal segment in particular, several tarsal, or metatarsal, bones may lengthen, the tail is long (for balance), and the dorsal vertebral column may be shortened and the pelvis strengthened in order to withstand the impact of landing (Hildebrand 1974, pp. 512–515). *Scleromochlus* displays all of these features and in addition, it has a deep intercondylar fossa (patellar groove) at the distal end of the femur (Huene 1914, p. 10), a feature seen in jumping mammals to accommodate a strong quadriceps femoris tendon. *Scleromochlus* may be compared with the jerboa and kangaroo rat which are similarly adapted and live in hot, sandy deserts. The suggestion by Huene (1914) that *Scleromochlus* climbed trees and made 'bold leaps from a branch' or even glided, is not likely since the feet hardly appear to be adapted for grasping branches. Likewise, the suggestion by Wilfarth (1949, pp. 7–9) that *Scleromochlus* lived underwater and used its powerful hindlimbs to propel itself to the surface for air, seems even less probable! *Scleromochlus* also appears to have some specific adaptations for living on sand, like the North American desert-living iguanid lizards *Uma* and *Dipsosaurus*: the nares are nearly closed by lateral flanges, there is a posterior flange from the squamosal and quadratojugal protecting the tympanic region, the lower jaw is 'countersunk', and the metatarsus is flattened.

The sedimentological and taphonomic data suggest that most of the Lossiemouth Sandstone Formation animals normally lived in well-vegetated areas, possibly around interdune pools or close to water outside the dune-field. During arid periods, large sand dunes migrated across the floodplain, and many of the animals may have been overwhelmed by the sand. Others died from natural causes within the area of dunes. Nevertheless, it is striking that no fossils have been preserved in the underlying water-laid beds, of animals like fishes, labyrinthodont amphibians, or phytosaurs.

The cadavers were normally buried rather rapidly by drifting sand dunes, which is suggested by their relatively well-articulated state. There may have been some scavenging of the carcasses by *Ornithosuchus* and the smaller carnivores.

AGE VARIATION AND SEXUAL DIMORPHISM

Stagonolepis, *Ornithosuchus*, *Hyperodapedon*, and *Leptopleuron* are represented by enough specimens to permit some observations on variation in size and proportions.

The material of *Stagonolepis* segregates into two size groups, each containing similar numbers of specimens. Individuals within each group are remarkably uniform in size, and all measurements differ by 25–30% between the groups. Proportions are similar in both groups and morphological differences slight. These groups have been interpreted as male and female animals (Walker 1961). Romer and Price (1940) found two size-groups in material of *Dimetrodon limbatus* and they also

explained these in terms of sexual dimorphism. Among living reptiles, male crocodiles and alligators tend to be larger than females of the same age (Guggisberg 1972, p. 127). Male lizards and tuataras also tend to be larger than females, but snakes often show exactly the opposite relationship (Goin and Goin 1971, pp. 115–116; Porter 1972, p. 309). Both situations may be found in chelonians.

Ornithosuchus displays a broad range of sizes, with estimated skull length ranging from 50 to 450 mm (Walker 1964, p. 57). These presumably represent age differences. A juvenile animal (BMNH R3149) shows proportional differences from larger specimens: relatively inflated cranium, short preorbital region, larger orbit, narrower interorbital region, upper temporal fossae diverge anteriorly and have a more medially placed process at the rear, and lack of posterior flanges of the parietals (Walker 1964, pp. 100–101).

The thirty-five specimens of *Hyperodapedon* display a range of sizes, with estimated skull length ranging from 125 to 210 mm, with the majority in the range 170–180 mm. One small fragment (RSM 1966.43.2) represents the tip of a juvenile dentary, but the other specimens cannot be segregated into distinct size-groups (Benton 1983*d*). Thus, as with *Ornithosuchus*, the size distribution corresponds to age alone. As is general among living reptiles, age size-classes may be apparent among juveniles, but they are usually blurred in older animals because of individual differences in growth rate (Gibbons 1976).

However, the material of *Hyperodapedon* may be divided into two classes according to proportions. For example, if two skulls of identical length are compared, certain 'important' elements (tooth-plate, occipital condyle, glenoid and quadrate facets) have the same dimensions, but bone bars and sheets between skull openings may differ markedly. Forms may be classified as 'gracile' or 'robust' on the basis of measurements of interorbital width, thickness of postorbital, or jugal, which differ by 20–70%. There is no relationship between these proportions and overall skull-size. It has been suggested (Benton 1983*d*) that the robust forms may be male, and the gracile forms female by analogy with certain living and fossil reptiles. The extant lizard *Lacerta jacksoni* shows sexual differences in the shape of the snout, nares, frontals, and occiput (Degen 1911). Proposed males and females of the dinosaur *Protoceratops* achieve the same maximum size, but differ in certain secondary sexual characters (frill, horn), as well as in the nasal height of the skull, size of the parietal fenestra, size of the nares, height of the coronoid process, and other features (Dodson 1976). Similarly, different skull patterns have been ascribed to sexual dimorphism in *Dimetrodon limbatus* (Romer and Price 1940), *Seymouria baylorensis* (Vaughn 1966), and *Tetragonias* (Cruikshank 1967).

Leptopleuron also shows well-marked 'robust' and 'gracile' forms independent of size. The type specimen (RSM 1891.92.528) is a small robust individual. These general findings in *Leptopleuron* are very similar to those in the related *Procolophon*. Broili and Schroeder (1936) found a range in skull sizes (lengths: 43–57 mm) and in robustness. The robust individuals had an additional horn-like process on the quadratojugal, and these were interpreted as males. There is some size variation in *Scleromochlus* also. Further study of the smaller Elgin reptiles is needed to establish the characters of age variation and sexual dimorphism.

DATING THE FAUNAS

The Hopeman Sandstone Formation

The footprints from the Hopeman Sandstone Formation (s.s.) are regarded as those of mammal-like reptiles, probably dicynodonts, and they closely resemble tracks from strata close to the Lower/Upper Permian boundary of Dumfriesshire, Penrith, and Mansfield (Hickling 1909; Watson 1909*b*; Watson and Hickling 1914; Haubold 1971; Smith *et al.* 1974). As noted already (p. 215), Glennie and Buller (1983) divided the Hopeman Sandstone Formation into two units, assuming that the contorted sandstones are confined to one horizon at about the same topographical level in the cliffs. However, since Williams (1973) recognized three well-separated horizons of contorted strata in upward succession from east to west, this assumption is open to question. Furthermore, the Clarkly Hill bore hole (Peacock *et al.* 1968, p. 130) encountered pebbly sandstone at the base of the Hopeman

Sandstone, many of the pebbles being faceted. This pebbly sandstone would naturally be taken to be the equivalent of the 'dreikanter bed' at the base of the Cutties Hillock Sandstone Formation, whereas Glennie and Buller correlate the upper of their two units with this formation. In addition, Glennie and Buller (p. 57) imply that the reptilian tracks occur in the lower of their two units, again if anything suggesting a correlation of this unit with the Cutties Hillock beds. The latter, however, are of very late Permian age. In fact, if we interpret Glennie and Buller correctly, the tracks would come predominantly from the upper of their two units, since they were most common in Masonshaugh, Greenbrae, and Clashach quarries. However, the evidence of the footprints cannot be regarded as very strong (see above), and the uncertainty over the succession within the Hopeman Sandstone Formation simply emphasizes the necessity for a separate Cutties Hillock Sandstone Formation in order to avoid confusion.

The Cutties Hillock Sandstone Formation

The reptiles from the Cutties Hillock Sandstone Formation were initially assumed to be of the same age as those from the Lossiemouth Sandstone Formation (Judd 1885, 1886*a*). However, Newton (1893) hinted that the faunas were distinct, and Taylor (1894) suggested a Permian age. Independently, Huene (1902) and Boulenger (1904) made the same suggestion. Walker (1973) discussed the age of the Cutties Hillock reptiles in detail, comparing *Elginia* and *Geikia* with animals from South Africa and Tanzania. He concluded that the Elgin formation was to be placed very close to the Permo-Triassic boundary, as had Watson and Hickling before him (1914), tentatively suggesting that it might lie at the very base of the Triassic, equivalent to a position low in the *Lystrosaurus* Zone of South Africa. The main evidence for this suggestion was that both *Elginia* and *Geikia* are more advanced than their closest relatives from the late Permian of South Africa and Russia, particular stress being laid on the specialization of the skull of *Elginia*. This view was not only based on the high degree of the spinescence, as stated by Rowe (1980), but reference was made to other skull characteristics. Rowe (1980) considered that the relationships of *Geikia* point to an uppermost Permian (i.e. *Daptocephalus* Zone) horizon for the Cutties Hillock Sandstone Formation. Using different evidence from that cited by Walker, Rowe confirmed that *Dicynodon locusticeps* (Huene, 1942), from the late Permian of Tanzania, is close to the ancestry of *Geikia*, and in fact referred *D. locusticeps* to the genus *Geikia*. He also showed that the close relatives of *Geikia*, the cryptodontid dicynodonts, all come from the late Permian of South Africa or Zambia. On the other hand, pareiasaurs less specialized in the skull than *Elginia* persist into the higher part of the *Daptocephalus* Zone (Kitching 1977), and there seems no reason why this group should have become extinct world-wide at the Permo-Triassic boundary. On balance, it seems best to take a conservative course, and regard the Cutties Hillock Sandstone Formation as lying at the extreme summit of the Permian, but bearing in mind that *Elginia* may represent a relict line which lingered on rather later in Scotland than elsewhere.

The Lossiemouth Sandstone Formation

The dating of the Lossiemouth Sandstone Formation has an even more involved history. The Elgin sandstones were all initially considered to be Devonian in age, until finds of reptile footprints and bones in the period between 1850 and 1860 convinced most palaeontologists that some of them must be regarded as younger. Local geologists long considered that the Lossiemouth sandstones were Devonian because they wanted to 'have' the oldest reptiles in the world (e.g. Phillips 1886; Gordon 1892). Also, certain geologists (e.g. Sir R. I. Murchison, Charles Lyell) had their own reasons for preferring to assign the reptiles to the Old Red Sandstone (Benton 1983*c*). However, Huxley (1867) argued convincingly for a Triassic age, and Murchison (1867, p. 267) accepted an Upper Triassic assignment.

Huene (1908) correlated the Lossiemouth sandstones with the German Lettenkohle (Late Ladinian) on the assumption that *Hyperodapedon* also occurred in the 'Lower Keuper' sandstone of the English Midlands together with amphibians and plants typical of the German formation.

However, the English material probably belongs to *Rhynchosaurus* (Walker 1969), and Huene's age assignment is not confirmed.

There is now strong evidence for a Lower Norian (Upper Triassic) assignment for the Lossiemouth Sandstone Formation. Walker (1961) pointed out that *Stagonolepis* is very closely similar to *Aetosaurus* from the German Stubensandstein (Middle Norian: Anderson and Cruickshank 1978; Tucker and Benton 1982). Aetosaurs occur also in the German Blasensandstein (*Ebrachosaurus* Lower Norian), the Dockum Group of Texas and the Chinle Formation of New Mexico and Arizona (*Desmatosuchus*, *Typhothorax*: L.–M. Norian), the Maleri Formation of India (un-named: L. Norian), the Ischigualasto Formation and Los Colorados Formation of Argentina (*Aetosauroides* and *Neoaetosauroides*, respectively: L. Norian and U. Norian/Rhaetian), and the New Haven Sandstone of Connecticut (*Stegomus*: M. Norian). *Aetosauroides* is slightly more primitive than *Stagonolepis* (Walker, in discussion to Warrington 1970, p. 218). *Ornithosuchus* is most closely related to *Riojasuchus* from the Los Colorados Formation of Argentina (Norian: Bonaparte 1978). *H. gordonii* is remarkably similar to *H. huxleyi* from the Maleri Formation of India, and *Scaphonyx* from the Santa Maria Formation of Brazil and Ischigualasto Formation of Argentina (all late Carnian or early Norian). The Elgin procolophonid *Leptopleuron* appears to be very close to *Hypsognathus* from the Newark Group of New Jersey (latest Triassic or earliest Jurassic: Olsen and Galton 1977). *Brachyrhinodon* is most like *Polysphenodon* from the Gipskeuper (Carnian) of East Germany (Walker 1966). The other Elgin reptiles do not appear to have had close relatives elsewhere, as far as we know.

The close relationship of *Hyperodapedon* from Elgin and India is important. The Maleri Formation has also yielded a primitive phytosaur close to *Francosuchus* from the German Blasensandstein (Lower Norian). The Maleri Formation fauna also contains specimens of the labyrinthodont *Metoposaurus* which is restricted to horizons in Germany ranging from the Schilfsandstein to the Blasensandstein (Upper Carnian–Lower Norian). The Maleri Formation is very probably Lower Norian in age, and the Lossiemouth Sandstone Formation also. Unfortunately the age of the Lossiemouth beds cannot be confirmed independently by means of other fossil groups.

The Lossiemouth Sandstone fauna shows some affinity with other northern hemisphere faunas of the late Triassic. It shares aetosaurs, sphenodontids, procolophonids and, coelurosaurs with the North American and German faunas. However, the Elgin beds lack the metoposaur amphibians and phytosaurs that dominate all of these faunas. The other elements of the Lossiemouth Sandstone fauna show affinities with India and the southern continents: similar late Triassic rhynchosaur are known from India and South America (a few scraps from North America), the closest relative of *Ornithosuchus* comes from South America, the South American and Indian faunas also have aetosaurs.

It is hard to find palaeogeographic reasons for these apparent distributional anomalies. The solution may depend on the environments in which the animals lived. The sediments in which the German, North American, and Indian faunas are found are largely water-laid, and metoposaurs and phytosaurs are clearly aquatic or semi-aquatic animals. However, the sediments of the South American formations are also largely water-laid, and amphibians are rare and phytosaurs are absent. The distinction between these two kinds of faunas is probably environmental, however, and they have been distinguished as a Metoposaur/Phytosaur Empire (Germany, North America) and a Rhynchosaur/Diademodontoid Empire (South America, ?Africa, ?India) (Tucker and Benton 1982; Benton 1983a). An interesting problem is the virtual absence of rhynchosaur in North America, and their complete absence in Germany which is hard to explain in view of their overwhelming abundance elsewhere.

SUMMARY

1. Fossil reptile remains are known from four horizons in the region of Elgin, north-east Scotland: the Hopeman Sandstone Formation, the Cutties Hillock Sandstone Formation, the Lossiemouth Sandstone Formation, and the Rhaetic.

2. The remains from the Hopeman Sandstone Formation of the coastal region are footprints of several kinds. These indicate a range of two or three genera of mammal-like reptiles as the producers, and they resemble other mid- to late-Permian trackways from elsewhere.

3. The reptiles from the Cutties Hillock Sandstone Formation include two dicynodonts, *Geikia* and *Gordonia*, a pareiasaur, *Elginia*, and an un-named procolophonid. These reptiles indicate a date in the late Permian near the Permo-Triassic boundary.

4. The reptiles from the Lossiemouth Sandstone Formation include the rhynchosaur *Hyperodapedon*, the thecodontians *Stagonolepis*, *Ornithosuchus*, *Erpetosuchus*, and *Scleromochlus*, the procolophonid *Leptopleuron*, the sphenodontian *Brachyrhinodon*, and the early dinosaur *Saltopus*. These reptiles individually suggest a late Triassic age, and jointly a lower Norian age.

5. The reptiles from the Rhaetic of Linksfield include plesiosaurs and crocodiles, represented by odd teeth, vertebrae, and limb bones.

6. The Cutties Hillock Sandstone Formation is formally defined here, and it is distinguished from the Hopeman Sandstone Formation. There is little evidence for a direct correlation of the two, and the new name is required to show the distinctness of the two formations.

7. The reptiles of the Cutties Hillock Sandstone Formation and the Lossiemouth Sandstone Formation occur in aeolian sediments. The skeletons are preserved fairly completely, and with only occasional disturbance (by predators?). The bone is sometimes preserved, and sometimes completely lost, so that casts can be made. There is good evidence that the skeletons occurred low in their respective formations, at the base of large aeolian dunes.

8. The Lossiemouth fauna includes medium-sized herbivores that must have fed in well-watered areas, as well as smaller lizard-shaped animals that show adaptations for running around in the dunes. For some genera there are enough specimens to show age variation and sexual dimorphism.

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MICHAEL J. BENTON

Department of Geology
The Queen's University of Belfast
Belfast BT7 1NN
Northern Ireland

ALICK D. WALKER

Geology Department
The University
Newcastle-upon-Tyne
NE1 7RU

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APPENDIX

Significant specimens of Elgin reptiles. Repository abbreviations are: BMNH, British Museum (Natural History); EM, Elgin Museum; GSE, Geological Survey Museum, Edinburgh; GSM, Geological Survey Museum, London; NUGD, Newcastle University, Geology Department; RSM, Royal Scottish Museum.

Hopeman Sandstone Formation footprints

Brickenden's (1850) slab: GSM 113445

Huxley (1859*b*, 1877): GSM (several slabs)

Undescribed: EM (6 slabs); RSM (several slabs); other material in Forres Museum; Inverness Museum and Manchester Museum

Cutties Hillock Sandstone Formation reptiles

Gordonia traquairi Newton 1893

GSE 4805-4806, 11703 (type specimen); GSM 58313-58318 (casts from type); (?)EM 1978.550

Gordonia huxleyana Newton 1893

GSE 4799-4802, 11704-11705 (type specimen); (?)EM 1978.549

Gordonia juddiana Newton 1893

EM 1890.3 (type specimen)

Gordonia duffiana Newton 1893

EM 1978.559.1, 2 (type specimen)

Geikia elginensis Newton 1893

GSM 90998-91015 (type specimen)

'dicynodont' (?*Gordonia*)

BMNH R4794; EM 1935.8, 1978.558, 886; RSM (Knock of Alves); RSM 1956.8.3, 1966.42.1-3, 1984.20.7

Elginia mirabilis Newton 1893

GSE 4783-4788 (type specimen), 4780-4781, 4791; EM 1978.546, 547, 548; RSM 1956.8.1-2

procolophonid

EM 1978.560; BMNH R4807(?)

Lossiemouth Sandstone Formation reptiles

Stagonolepis robertsoni Agassiz 1844

EM 1858.10 (type specimen); other material is listed in Walker (1957, 1961), plus Manchester Museum L8265, L8267; RSM 1952.10.2, 1966.43.3, 9; Glasgow Museum, Kelvingrove G66, 41aj-as; Tübingen unnumb.

Hyperodapedon gordoni Huxley 1859

EM 1978.566.1-2 (type specimen); other material is listed in Benton (1983*d*)

Ornithosuchus longidens (Huxley 1877)

BMNH R2409-2410 (type specimen of *Ornithosuchus woodwardi*); EM 1978.570-571 (type specimen of *Dasygnathus longidens*); other material is listed in Walker (1964)

Erpetosuchus granti Newton 1894

BMNH R3139 (type specimen); (?)RSM 1966.43.4; NUGD unnumb.

Saltopus elginensis Huene 1910

BMNH R3915 (type specimen)

Leptopleuron lacertinum Owen 1851

RSM 1891.92.528 (type specimen), 1966.43.7, 10; BMNH R3136, R3144, R3145, R3147, R3362, R3363, R3365, R3558, R3917, R3918, R3919, R3920, R3922, R3923, R3924, R3925, R3926, R3927, R3928, R3930, R3931, R4779; EM 1920.5, 1978.718, 726, 727.1-3; GSM (91079, 91082-91084, 91087-91088, 91093); RSM.GY.1984.20.34; Tübingen PV18415

Brachyrhinodon taylori Huene 1910

BMNH R3559 (type specimen), R3364, R3921, R3929, R4776, R4777, R4778; EM 19-21 (+42?), 24-27, 30-31; RSM 1966.43.6, 8

Scleromochlus taylori Woodward 1907

BMNH R3556 (type specimen), R3146, R3557, R2914, R4823, R4824, R5589

Unidentified thecodontian

MM L8270

NOTE ADDED IN PROOF

The bone from Crownhead Quarry (see p. 217) is now numbered Forres Museum L1978-42ak. The footprint from Cutties Hillock figured by Watson and Hickling (1914, fig. 1) is in the Manchester Museum (MM L10275).